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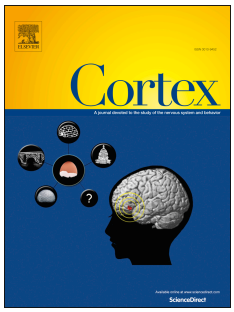

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Cross-Modal Transfer of Statistical Information Benefits from Sleep

(Running Title: Cross Modal Transfer Benefits from Sleep)

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Abstract

Extracting regularities from a sequence of events is essential for understanding our environment. However, there is no consensus regarding the extent to which such regularities can be generalised beyond the modality of learning. One reason for this could be the variation in consolidation intervals used in different paradigms, also including an opportunity to sleep. Using a novel statistical learning paradigm in which structured information is acquired in the auditory domain and tested in the visual domain over either 30min or 24hr consolidation intervals, we show that cross-modal transfer can occur, but this transfer is only seen in the 24hr group. Importantly, the extent of cross-modal transfer is predicted by the amount of SWS obtained. Additionally, cross-modal transfer is associated with the same pattern of decreasing MTL and increasing striatal involvement which has previously been observed to occur across 24 hours in unimodal statistical learning. We also observed enhanced functional connectivity after 24 hours in a network of areas which have been implicated in cross-modal integration including the precuneus and the middle occipital gyrus. Finally, functional connectivity between the striatum and the precuneus was also enhanced, and this strengthening was predicted by SWS. These results demonstrate that statistical learning can generalise to some extent beyond the modality of acquisition, and together with our previously published unimodal results, support the notion that statistical learning is both domain-general and domain-specific.

Introduction

One way in which we attempt to make sense of our environment is by observing and generalising from predictable patterns in sequences of events. In recent years, such statistical learning has been demonstrated not only in the auditory domain using syllables (Saffran et al. 1996; Pelucchi et al. 2009) and tones (Saffran et al. 1999; Durrant et al. 2013), but also in the visual domain using abstract symbols (Fiser and Aslin 2001; Turk-Browne et al. 2008). It has been shown in infants (Saffran et al. 1996), adults (Saffran et al. 1999), and even non-human primates (Hauser et al. 2001).

A key aspect of our perceptual relationship with the environment is the fact that it is multi-modal. An important consequence of this is that information gleaned in one modality is potentially useful in other modalities, and that raises an important question for learning theory: to what extent does something learned in one modality transfer to another? This question has received attention in recent years, primarily using paradigms of artificial grammar learning (Gómez et al. 2000) in which a Reber grammar (Reber 1967) is learned in one modality, and is tested in another modality. However, there remains no consensus on the extent to which this is possible (Vouloumanos et al. 2012), with some studies showing a high level of transfer between modalities (Altmann et al. 1995) and others suggesting little if any transfer takes place (Conway and Christiansen 2006). Part of the reason for this is that the related question of what transfers – episodic repeated fragments or abstract transition statistics – also remains disputed (Perruchet and Pacteau 1990; Tunney and Altmann 2001).

One reason for the lack of consensus could be that essential elements involved in cross-modal transfer are not included in most paradigms. In particular, memory consolidation, and the specific role of sleep in memory consolidation, could play an essential role in abstraction from one modality to another. We previously showed that abstraction of underlying statistical structure was enhanced after consolidation across sleep and predicted by the time spent in slow wave sleep (SWS) (Durrant, Taylor, et al. 2011). SWS also predicted a trade-off between recruitment of medial temporal lobe (MTL) and striatum during

subsequent use of this knowledge (Durrant et al. 2013). Based upon these data and a growing literature supporting the role of sleep in other forms of abstraction (Wagner et al. 2004; Gómez et al. 2006; Djonlagic et al. 2009; Walker and Stickgold 2010), we hypothesise that sleep, and especially SWS may also facilitate the cross-modal transfer of abstract statistical knowledge.

To test this hypothesis, we presented participants with a long sequence of auditory tones which contains an underlying probabilistic structure, and then tested their ability to recognise this probabilistic structure in a set of auditory stimuli (to test unimodal statistical learning, reported in Durrant et al 2013) and a set of visual stimuli (to test cross-modal transfer, reported here). One group of participants had a retention interval of just 30min between the exposure and final test sessions, while another had an interval of 24hrs including overnight sleep, which was monitored with polysomnography. We used functional magnetic resonance imaging (fMRI) to look at the underlying networks employed in the task, and differences in neural organisation as a result of consolidation and sleep. Based on our findings with respect to unimodal consolidation of these stimuli (Durrant et al. 2013) we expected greater involvement of the medial temporal lobe in the 30min group (that had little time to consolidate) and greater involvement of the striatum in the 24hr group. We also expected the interplay between these regions would be modulated by slow wave sleep.

Materials and Methods

Participants

Forty participants were randomly allocated to two experimental groups (30min and 24hr). 4 participants were excluded due to insufficient sleep (< 4 hours), equipment malfunction, brain abnormality, or excessive head movement, leaving 18 participants (9 male and 9 female, aged 24.2±1.3) in the 30min group and 18 participants (9 male and 9 female, aged 23.8±0.8) in the 24hr group. All were right-handed (>80% on the Edinburgh Handedness Inventory), had no history of neurological or sleep disorders, and were taking no medication except the contraceptive pill. Participants were asked to abstain from alcohol, caffeine and other drugs, and to refrain from napping, throughout the entire period of the experiment. All participants gave informed consent for the experiment, which was approved by the Research Ethics Committee of the School of Psychological Sciences at the University of Manchester and the Research Ethics Committee of the University of Liverpool.

Stimuli

The stimuli consisted of an auditory exposure sequence, 84 auditory test sequences and 84 visual test sequences. Auditory stimuli were sequences of pure tones, each of which was drawn from seven possible pitches defined by frequencies 261.63Hz, 288.86Hz, 318.93Hz, 352.12Hz, 388.77Hz, 429.24Hz and 473.92Hz, which were obtained by dividing an octave into seven equal intervals in pitch space. Tones lasted 200ms with a 20ms gap between them, and were sampled at 44100Hz with a fixed amplitude and Gaussian modulation to reduce aliasing effects. The auditory exposure sequence was 1818 tones long, while each of the short test sequences lasted just 18 tones.

Analogous to the auditory stimuli, the visual stimuli were sequences of a yellow circle moving from left to right across a black background (back-projected onto a screen with a resolution of 1024 x 768 pixels). The circle started in a location 62 pixels from the left edge of the screen, where it remained for 200ms. It then disappeared for 20ms and appeared in its next location 53 pixels to the right, where it again remained for 200ms. This process continued for 18 horizontal locations, thus giving the appearance of a circle moving across

the screen in a series of discrete events (see **Supplementary Video** online). The vertical position for each event could take one of seven evenly spaced vertical locations (-250 pixels, -166.67 pixels, -83.333 pixels, 0 pixels, 83.333 pixels, 166.67 pixels, 250 pixels, relative to the centre of the screen). The seven vertical locations were chosen in analogy with the seven possible pitch height locations in the auditory sequence. The visual stimuli was designed to be directly analogous to the auditory sequences, which also consisted of discrete events over time, of the same duration, and with the same possible variations in height. Participants were, however, not told of this analogy; nor were they aware of how the sequences (auditory or visual) were structured. In order to prevent participants from using auditory imagery (i.e. imagining an auditory analogue to the visual sequences in their head), random auditory tones (of the same duration and drawn from the same seven frequencies) were played while the visual sequence was being presented, and participants were told to ignore those tones and use only the visual information in their judgment.

The auditory encoding sequence, 42 of the auditory test sequences and 42 of the visual test sequences, shared an underlying statistical structure with respect to the sequence pitch/vertical positions (structured condition), while the other 42 auditory test sequences and 42 visual test sequences were random (random condition). This structure was given by a first-order transition matrix containing the probabilities for each potential transition between the current pitch/vertical position and the next pitch/vertical position. In our transition matrix (shown in Table 1), each row contained one likely transition (p=0.9) and six unlikely transitions (p=0.0167). This means that any given pitch/vertical position is followed by another specific pitch/vertical position 90% of the time, but deviates from this pattern 10% of the time, making the structured sequences probabilistic. By contrast, in the random condition, pitch/vertical position was chosen at random from the seven possible locations without reference to the transition matrix.

[TABLE 1 HERE]
[FIGURE 1 HERE]

Experimental Task and Design

The experiment consisted of two sessions (see Figure 1). Participants in the 30min group undertook the first session at 2pm (+/- 1 hour) and after a 30min delay were placed in the fMRI scanner where they undertook the second session (starting the task around 3pm). Participants in the 24hr group also undertook the first session at 3pm (+/- 1.5 hours) and subsequently slept overnight from 11.30pm to 7.30am in a bedroom in the Sleep Research Laboratory at the University of Manchester, where they were monitored with PSG while they slept. After leaving the lab the following morning (day 2), they went about their normal daily activities (which did not include anything physically or mentally strenuous such as sporting activities or exams), returning to the lab to undertake the second session at 3pm (+/- 1.5 hours) that afternoon (controlled to ensure the consolidation interval for any individual was limited to 24hrs +/- 0.5 hours). Subsequent behavioural analysis suggested that the small variation in the time of the first session (necessary to ensure that the second group had 24hrs consolidation and that both groups were scanned at the same time) made no difference to the results.

Participants were told about the two-session structure, but not that the sequences had an underlying statistical structure. They were also not told about the relationship between auditory and visual sequences, or even that they would encounter any visual stimuli, which were left as a surprise test.

During the first session participants passively listened to the auditory exposure sequence and undertook an initial test of 84 auditory trials as described in our previous paper (Durrant et al. 2013). During the second session, which took place inside an fMRI scanner, participants first undertook another 84 auditory test trials. On 84 subsequent trials, participants were presented with visual test sequences and were instructed "Please indicate whether or not a sequence feels similar to the auditory exposure sequence", and were told that half the trials would be similar and half not similar (in order for participants to develop a consistent benchmark of similarity). Written instructions and the trial number were presented prior to each trial. An additional 21 trials were rest trials that included no task; activation in these trials provided an fMRI baseline. Each trial lasted approximately 9s, including a 5s response window. Participants were told of the 5s response window but instructed to respond as quickly as possible while maintaining accuracy. Trial order was randomised for each participant. After the experiment, participants were verbally debriefed, which included a question asking how difficult they found it, a question asking about the nature of any similarity identified and an open question for any further information.

Polysomnography

Polysomnography (PSG) was carried out on all participants in the 24hr group using an Embla© N7000 sleep monitoring system. The scalp was prepared with NuPrep© exfoliating agent and Ag-AgCl electrodes were then attached using EC2© adhesive electrogel and medical tape. Scalp electrodes were attached at C3, C4, F3, F4, O1 and O2 locations using the 10-20 system. Each was referenced to the contralateral mastoid (A1 and A2). In addition, left, right and upper electromyogram, left and right electrooculogram and a ground electrode were also attached. All electrodes were verified to have a connection impedance of less than 5kOhms and all signals were digitally sampled at a rate of 200Hz.

fMRI data acquisition.

Functional and structural MRI data were acquired using a 3T Allegra MR scanner (Siemens, Erlangen, Germany) with an 8-channel head coil. Functional time series consisting of T2*-weighted images were obtained with a gradient echo-planar sequence giving a Blood Oxygen Level Dependent (BOLD) signal. 50 transaxial slices were acquired in an ascending sequence with a voxel size of 3 x 3 x 2.8 mm^3 including an interslice gap of 40%, tilt of 15°, flip angle of 80°, matrix size of 64*64, TR of 2960 ms and TE of 30ms. A T1-weighted structural image was acquired in the same session for each participant using a 3D IR/GR sequence with 1mm^3 cubic isovoxels, a flip angle of 8°, matrix size o f 224 x 256 x 176, TR of 2040ms and TE of 5.57ms.

Behavioural Data Analysis

On each trial, participants gave a single response indicating whether or not the sequence seemed familiar. Performance was measured with the sensitivity index d' in order to account for any response bias, calculated as d' = z(hits)-z(false alarms). In cases with maximum hits or no false alarms, we adopted the common practice of adding the equivalent of half a trial (0.5/84) to the proportion correct to avoid division by zero (Stanislaw and Todorov 1999). The d' scores within each session were analysed with an independent-samples t-test comparing the 30min and 24hr groups, which was the principal measure of interest. Given the perceived difficulty of the visual task, we also conducted one-sample t-tests against chance level (a d' score of 0) for both groups in that task.

Alertness Analysis

When examining potential effects of sleep, it is important to check for potential differences in alertness which might contribute to those effects. Participants also gave a subjective measure of alertness at the start of both test sessions using the Stanford Sleepiness Scale (SSS)(Glenville and Broughton 1978). This was analysed using a 2-way mixed ANOVA with factors of session and group. In addition, response times were used as an objective measure of alertness. Previous research has suggested that in statistical learning tasks, in common with many other behavioural tasks, correct responses are generally faster than incorrect responses (Kim et al. 2009). Similarly, both accommodation and task familiarity/practice effects would suggest that response times should be faster in the second session. However, there should be no differences between the groups on these measures unless is there a confounding factor. We therefore conducted a 2-way mixed ANOVA on response times in each session separately with factors accuracy (correct, incorrect) and group (30min, 24hr); this analysis allowed us to detect any difference in response times between the groups, and whether or not this was due to overall performance differences (i.e. if these were driven by more correct responses in the 24hr group).

PSG Data Analysis

Sleep data was recorded and analysed using RemLogic© 1.1 software. Following the standard approach to sleep scoring (Rechtschaffen and Kales 1968), the data were organised into 30s epochs, bandpass filtered between 0.3Hz and 40Hz to remove low frequency drift and high frequency noise, and visually scored independently by two experienced sleep researchers on the referenced central electrodes (C3-A2 and C4-A1) using standardised sleep scoring criteria. As a relationship between consolidation of statistical information and SWS has previously been found (Durrant, Taylor, et al. 2011; Durrant et al. 2013), an *a priori* hypothesis led to a planned correlation looking at the relationship between the behavioural performance on the visual task (visual d') and the amount of SWS obtained. In addition Bonferroni-corrected correlation tests between the other sleep stages (N1, N2, REM) and visual d' were also carried out to fully characterise the sleep-behaviour relationship.

fMRI Data Analysis

Functional imaging data was processed using SPM8 software (http://www.fil.ion.ucl.ac.uk/spm/). Functional images were realigned to correct for motion artefacts and corrected for slice acquisition time differences, coregistered with a structural image, normalised to MNI space and smoothed using a Gaussian kernel with a FWHM of 8mm.

Analysis used a two-level random effects general linear model (GLM) (Friston et al. 1995). The design matrix for each participant at the first level had separate boxcar regressors for structured and random sequences; these regressors were mini-blocks of approximately 4s, coinciding with the onset and offset of each stimulus sequence. To avoid performance confounds only trials with correct behavioural performance were included. Incorrect trials, button presses and movement artefacts were modelled as regressors of no interest.

First-level one-sample t-tests for each structured and random regressor provided contrast images for a second-level mixed ANOVA. This focused on the interaction of consolidation and structure and contained factors group (30min, 24hr) and structure (structured, random). *A priori* volumes of interest (VOIs) in medial temporal lobe (hippocampus and parahippocampus) and striatum (caudate and putamen), created with automatic anatomical templates (Tzourio-Mazoyer et al. 2002) as implemented in the WFU-

Pickatlas software (Maldjian et al. 2003) and based on previous results related to statistical learning and sleep (Durrant, Taylor, et al. 2011; Durrant et al. 2013), were examined. Whole brain analyses adopt the standard convention of showing results at p=0.001 (uncorrected), while VOI analyses were family-wise error-corrected at p<0.05 using Gaussian random field theory (Worsley et al. 1996). In both cases a minimum extent threshold of k=5 voxels was adopted to ensure that reported clusters are robust and functionally significant and to facilitate comparison with our previously-reported results (Durrant et al. 2013) which took the same approach.

To examine the possibility that some of the neural activation related to consolidation was associated with specific sleep stages, we performed a regression analysis in SPM8. First-level contrast images revealing activation related to correctly processing the structured sequences [structured > random] were used in a second-level design matrix with a constant regressor ([structured > random]) and three parametric regressors [%S2, %SWS, %REM].

In addition to identifying localised differences in activation, we examined the functional connectivity between regions using psychophysiological interactions (PPIs). Two separate PPI analyses were performed with seed regions centred in left putamen (-18,11,1) and left perirhinal cortex (-18,-7,-29) respectively; these coordinates were peaks of the group response to the [structure > random] contrast in our localisation analyses, which is the standard approach in PPI analysis. It ensures that the functional relationships examined (i.e. physiological activation correlations which are mediated by the condition of interest in the experiment, which in this case is sequence structure) involve regions which have been identified as being involved in the task.

The physiological factor of the PPI was created by extracting and deconvolving the timecourse of activity for those voxels within the seed region which were activated in the [sequence > baseline] contrast at p<0.001 to ensure only voxels involved in processing the sequences were included. Our psychological factor was the contrast [structure > random]. First-level contrasts were carried forward to a second-level random effects analysis comparing the 30min and 24hr groups.

Results

Auditory Results

The auditory task was designed to answer the questions: does statistical learning consolidate across sleep, and if so what is the neural basis of this? The visual task was designed to answer the complementary questions: does statistical learning from one modality (auditory) transfer to another (visual), is this dependent on intervening sleep, and if so what is the neural basis of this? Due to this conceptual difference, the fact that the auditory task was always performed before the surprise visual task (and so could not have been influenced by it) and the large amount of behavioural, alertness, sleep and imaging data to be described for each study, it was strongly preferable to report the results of the auditory statistical learning task in a separate paper, which we have done (Durrant et al. 2013). However, we are conscious that performance on the auditory task could conceivably have influenced subsequent performance on the visual task, and is in any case informative in terms of interpreting performance on the visual task, so we have included those results in our main table of behavioural results (Table 2) to facilitate comparison. We have also analysed the relationship between auditory and visual results within-subject, and provide the results in a later section here. For all other results with regard to the auditory statistical

learning task we refer the reader to our previous paper (Durrant et al. 2013), and concentrate here on analysis of the visual task performance.

[FIGURE 2 HERE]
[TABLE 2 HERE]

Behavioural Performance
The main behavioural results can be seen in Table 2. Both groups showed similar learning of the underlying statistical structure, demonstrated by equivalent performance in the initial auditory test (session 1). However, the group which had 24 hours consolidation interval showed significantly better performance on the visual test in session 2, in comparison to the group which had only 30 minutes ($t(34) = 2.03$, $p < 0.05$; see Figure 2). In particular, participants in the 24hr group were able to generalise their statistical knowledge across modalities from the initial auditory exposure sequence to the visual test, performing significantly above chance in the latter ($t(17) = 3.98$, $p < 0.001$). By contrast, participants in the 30min group showed no evidence of cross-modal generalisation, performing only at chance level ($t(17) = 1.58$, $p = 0.133$).

[TABLE 3 HERE]

Polysomnography
The polysomnography data is shown in Table 3. The 18 participants had an average sleep onset time of 11:59pm ± 10.47 minutes and slept for more than 7 hours on average (421.58 ± 12.98 minutes). Participants spent 46.66 ± 5.53 minutes in stage 1 sleep, 199.65 ± 10.98 minutes in stage 2 sleep, 88.79 ± 5.67 minutes in SWS and 86.63 ± 9.04 minutes in REM sleep. These figures are typical of a healthy young adult population (Ohayon et al. 2004; Carskadon and Dement 2011), except for a small increase in stage 1 which is typical of laboratory studies (Lorenzo and Barbanoj 2002).

To allow comparison with our previous report and to control for differences in total sleep duration which may influence duration-based correlations, the proportions of overall sleep time spent in different sleep stages were our measures of principal interest. The average proportion of time spent in stage 1 sleep (11.34 ± 1.45%), stage 2 sleep (46.92 ± 1.55%), SWS (21.74 ± 1.87%) and REM sleep (20.04 ± 1.79%) were again generally typical of a healthy young adult population.

There was a moderately strong and significant correlation between SWS % and behavioural performance on the visual task ($r(18)=0.502$, $p=0.034$; see Figure 2B), suggesting that SWS was actively involved in allowing generalisation to a different modality. N1 sleep % ($r(18)=-0.234$), N2 sleep % ($r(18)=-0.328$) and REM sleep % ($r(18)=-0.049$) showed no such relationship with behavioural performance (all $p>0.3$ after correction for multiple comparisons across the correlation tests). It is worth noting this was pattern was also repeated for absolute durations, with SWS again showing a relationship with performance ($r(18)=0.557$, $p=0.016$), while other sleep stages showed no such relationship (N1 sleep: $r(18)=-0.314$); N2 sleep: ($r(18)=-0.274$); REM sleep: ($r(18)=-0.075$)).

Alertness
Results from the Stanford Sleepiness Scale showed no effect of session ($F(1,34)=0.145$, $p=0.705$), no effect of group ($F(1,34)=0.017$, $p=0.897$) and no interaction between these ($F(1,34)=1.308$, $p=0.261$), suggesting that subjective sleepiness was not a confounding variable within the study.

As expected, response times in the first session were faster for correct (1.029±0.084) than incorrect (1.232±0.093) responses; this effect was significant $F(1,34)=36.115$, $p<0.001$). However, there was no effect of group on response time ($F(1,34)=0.228$, $p=0.636$) and no interaction between group and accuracy ($F(1,34)=0.003$, $p=0.953$), confirming that in the first session response times revealed no differences in alertness between the groups for any type of trial. Response times (shown here in seconds) in the second session followed the same pattern, with an effect of correctness ($F(1,34)=10.838$, $p=0.002$) with faster responses for correct (0.877±0.053) than incorrect (0.966±0.060) items, but no effect of group ($F(1,34)=1.773$, $p=0.192$) and no interaction ($F(1,34)=0.128$, $p=0.723$).

Collectively, these subjective and objective measures of alertness suggest that there were no differences between the groups which could otherwise account for the results.

[TABLE 4 HERE]

fMRI Localisation

Participants were scanned with fMRI during the visual test sequences in order to look for differences in brain activity between the two groups which might account for their different behavioural performance or be related to the amount of sleep obtained. Data were analysed at the second-level with a 2 x 2 mixed ANOVA with factors group (30min, 24hr) and sequence (learned probabilistic structure, random).

The main effect of structure (for correctly-identified sequences) revealed an extensive network of activation (listed in Supplementary Table S1), including visual areas such as left inferior, left superior and right middle occipital gyri, auditory areas such as left superior and left middle temporal gyrus, motor areas centred on the right precentral gyrus and the supplementary motor area, declarative memory areas including bilateral hippocampus, and non-declarative memory areas including bilateral putamen. One-tailed t-tests conducted in SPM8 revealed all of this activation to be greater for structured than random sequences; no activation was greater for random sequences. These findings are in keeping with our previous auditory findings (Durrant et al. 2013) as well as those from other groups looking at unimodal visual statistical learning (Turk-Browne et al. 2010). VOI analysis (small volume FWE-corrected at p=0.05) focusing on the medial temporal lobe and striatum (shown in Table 4) revealed activation in the left hippocampus (-24,-16,-17), left putamen (-15,11,-2) and right putamen (18,8,-5). Again, all of this activation was greater for structured sequences, and all of it fits well with previous evidence that suggests both the medial temporal lobe and the striatum play a significant role in identifying sequences with a common statistical structure (Turk-Browne et al. 2009).

[TABLE 5 HERE]
[FIGURE 3 HERE]

Neural differences related to consolidation of structured information obtained from the auditory exposure sequence, and in particular transfer of that knowledge into the visual domain, is given by the interaction term of the ANOVA, which shows how task-related activation differs between the two groups. Whole brain analysis (shown in Table 5) at $p=0.001$ (uncorrected) revealed active areas in left and right parahippocampus, the left putamen, and the middle temporal gyrus. Of these, the clusters in the left parahippocampus (-18,-7,-29), which is located specifically in the left perirhinal cortex, and the left putamen (-18,11,1) (shown in Supplementary Table S2 and indicated with * in Table 5) survived FWE correction in *a priori* VOI analysis which used automatic anatomical templates (Tzourio-

Mazoyer et al. 2002) of bilateral medial temporal lobe (hippocampus, parahippocampus) and bilateral dorsal striatum (caudate and putamen) as the search volumes. Further analysis of the interaction (shown in Table 5 and Figure 3) in these two clusters reveals opposite patterns. The cluster in the left perirhinal cortex is positively activated for structured (relative to random) sequences prior to consolidation (30min group). For participants who have had an opportunity to consolidate (24hr group), however, the left perirhinal cortex is deactivated for structured sequences. By contrast, the cluster in left putamen shows positive activation for structured sequences for participants who have time to consolidate their statistical learning (24hr group), but no activation above baseline for random sequences. The 30min group show no activation above baseline for either structured or random sequences in this area. Taken together, these results present a pattern of activation in which the left perirhinal cortex is involved in correctly recognising probabilistically structured sequences prior to consolidation (beyond the first 30 minutes), and the left putamen takes over this function across the ensuing 24 hours. The consolidation interval included a night of sleep; however, regression analysis revealed no significant relationship between the individual sleep parameters and activation in these areas (no significant voxels).

[TABLE 6 HERE]
[FIGURE 4 HERE]

fMRI Connectivity

In addition to analysing individual areas of activation, the task-related functional connectivity between different areas was examined using psychophysiological interactions (PPIs; see Table 6 and Figure 4). Seeds were placed at the peak of the two areas (left putamen and left perirhinal cortex) found to be involved in consolidation of structured information according to the localisation analysis discussed above. Functional connections stronger in both the 24hr and 30min groups for structured than random sequences were found between the left perirhinal cortex (-18,-7,-29) seed, two clusters bilateral precuneus (-9,-61,34/9,-58,34 and 3,-37,42/3,-43,43) with both in the anterior subdivision of Cavanna et al (2006), and bilateral postcentral gyrus (-57,-13,46 and 60,-7,40). No functional connections between the left perirhinal cortex and any brain area were stronger for random sequences. The left putamen (-18,11,1) seed had a functional connection to a visual processing area in right middle occipital gyrus (45,-76,10), stronger in both groups for structured than random sequences. Interestingly, the strength of functional connectivity between the left putamen seed and the first bilateral precuneus cluster (in this case centred on -12,58,34) which showed a functional relationship with the left perirhinal cortex, was predicted by the amount of SWS obtained ($r(18)=0.744$, $p<0.001$) and was associated with stronger task performance ($r(18)=0.499$, $p=0.035$). Again, no functional connections between the left putamen and any other brain area were revealed to be stronger for random than structured sequences.

Comparison of Auditory and Visual Results

One of the benefits of using the same participants in the auditory and visual tests is that it allows a within subject comparison of performance on the two modalities in order to provide a deeper understanding of how the visual results are related to the auditory results. Performance in the auditory test session following the consolidation interval was only mildly (and non-significantly) correlated with performance in the visual test session which took place immediately afterwards ($r(36)=0.187$, $p=0.286$). This was more strongly the case for the 24hr group ($r(18)=0.146$, $p=0.564$) than the 30min group ($r(18)=-0.049$, $p=0.846$), though

the two correlations were not significantly different (Fisher's z=0.537, p=0.589). Overall, performance in the auditory test was not a particularly good predictor of performance in the visual test.

The relative independence of the auditory and visual behavioural performance raises the possibility that functional brain responses associated with the auditory and visual task might also be largely independent. On the other hand, the similar pattern of group-level results between the modalities suggests a possible common cause. To test this, we extracted parameter estimates for the two significant clusters for the sleep x structure interaction (left putamen and left perirhinal cortex) for both auditory and visual conditions in each participant. We then tested for correlations between auditory and visual parameter estimates in each case. It should be noted that the exact coordinates of the clusters differed slightly between the auditory and visual conditions; however, the correlation tests the hypothesis that neural activation relevant to the study is driven by a common mechanism in the auditory and visual conditions, such that a participant with stronger task-specific activation in one condition will show stronger task-specific activation in the other condition. A marginally significant correlation (r(72)=0.210, p=0.077) between the two left perirhinal cortex clusters (-21,-25,-23 in auditory and -18,-7,-29 in visual conditions) and a significant correlation (r(72)=0.251, p=0.034) was also found between the two left putamen cortex clusters (-24,17,5 in auditory and -18,11,1 in visual conditions). As with the behavioural results, the positive correlations were driven by the 24hr group which showed significant correlations for both the left perirhinal cortex (r(36)=0.374, p=0.025) and the left putamen (r(36)=0.406, p=0.014). By contrast, the 30min group did not show a significant auditory-visual correlation in either the left perirhinal cortex (r(36)=0.177, p=0.302) or the left putamen (r(36)=-0.294, p=0.082). Taken together, these correlations were slightly stronger (and more consistent) than the behavioural correlations while following the same broad pattern, and suggest a neural substrate underpinning the task across the two modalities that is partly shared and partly independent.

Discussion

This study was concerned with cross-modal transfer of statistical learning, how this may be dependent on sleep, and the underlying neural substrates. Using a novel statistical learning cross-modal transfer task, we offer behavioural evidence of auditory to visual transfer of statistical knowledge following a 24hr consolidation interval. Polysomnography shows that this transfer is related to the amount of slow wave sleep obtained during the consolidation interval. Neuroimaging shows activation in the medial temporal lobe for participants with only a 30min consolidation interval, and increased activation in the striatum for those with a 24 hour delay including a night of sleep. Functional connectivity analysis revealed the engagement of a multimodal integration network including the precuneus and the middle occipital gyrus, part of which also showed a dependence on slow wave sleep. Taken together, these results confirm the importance of sleep for abstracting statistical information and applying it in another modality.

To what extent can information learned in one modality be applied in another? This key question remains hotly contested and goes to the heart of the debate concerning the extent to which statistical learning is domain-specific rather than domain-general (Saffran and Thiessen 2006; Walk and Conway 2008; Sloutsky 2010; Thiessen 2011). There is a widespread belief that statistical learning within a given modality is necessary for language learning (Thompson and Newport 2007; Yeung and Werker 2009; Conway et al. 2010;

Arciuli and Torkildsen 2012) as well as other related phenomena such as music enculturation (Brandt et al. 2012). However, there is less consensus that this learning transfers beyond the learning modality, with a variety of studies, usually deploying Reber grammars (Reber 1967) in one or more modalities, leading to radically different conclusions. For example, Conway et al (2006) report that learning two grammars in visual and auditory modalities respectively, which were subsequently tested in just one modality, showed no performance loss as a result of interference between the two grammars as long as they were learned in different modalities. Learning two grammars within a modality did lead to reduced performance; taken together, these results were interpreted as evidence of separate visual and auditory processing, and hence of stimulus-specific rather than abstract representations. On the other hand, a series of experiments also using a Reber grammar task (Altmann et al. 1995), found good evidence of transfer from various configurations of tones, spoken syllables or graphics symbols to letters, graphical symbols or written symbols. To some extent this is a difference in tone and perspective; both sets of results can be interpreted as showing some transfer across modalities, but performance within the training modality remaining stronger.

The above studies, together with many similar ones, use artificial grammar learning. Although closely related to statistical learning (Perruchet and Pacton 2006), there are important differences (artificial grammars usually contain explicit rules, while statistical learning is based on transition probabilities), and this could potentially influence transfer. A recent statistical learning study by Vouloumanos et al (2012) used the Saffran paradigm (Saffran et al. 1996, 1999) in which a stimulus stream can be segmented into distinct units based on the transition statistics, and the task involves abstraction and identification of those units. Transfer to new stimuli with acoustically different properties (but still within the auditory domain) was seen in this study, but performance was weaker than for the original stimulus set. Similarly, a study looking at multisensory integration of statistical learning found that performance was impeded when multiple stimulus streams in different modalities presented conflicting segment boundaries, suggesting that they were not being encoded in an entirely modality-specific manner (Mitchel and Weiss 2011). However, ours is, to the best of our knowledge, the first study using a statistical learning paradigm (rather than artificial grammar learning) which explicitly examines the question of transfer from one modality to another.

Our data show that transfer from the auditory to the visual domain is possible, but is only seen in the group which had a 24hr consolidation interval. There are three possible interpretations of this. The first is that the task overall was very difficult (something reported by all participants). A previous study of transfer in artificial grammar learning reported that successful transfer was amongst other things dependent upon good initial learning (Bly et al. 2009). It is therefore possible that the chance level results seen in the 30min group are a floor effect related to the task difficulty and that had the task been easier, they may have shown some transfer (though presumably still less than the 24hr group). A second possibility is that transfer requires time to consolidate. However, the significant correlation with SWS, something also seen in the unimodal auditory results (Durrant et al. 2013), points towards a third possibility – that transfer requires sleep. In fact, it is likely that all three make a contribution; immediate transfer to some extent is likely based on the studies described above, and previous evidence has supported a role for both time and sleep in consolidation of statistical learning (Durrant, Cairney, et al. 2011). Our results therefore add to the growing literature on sleep-dependent or sleep-enhanced abstraction (Wagner et al. 2004; Gómez et al. 2006; Djonlagic et al. 2009; Walker and Stickgold 2010). These data support the suggestion that SWS plays a role in abstracting common underlying statistical patterns

from diverse stimuli (Lewis and Durrant 2011) and transferring them even across modality boundaries.

Given evidence of cross-modal transfer, another important question arises: what has transferred? Another ongoing debate in both statistical learning and artificial grammar learning concerns the nature of the task and the representations used by participants (Perruchet and Pacteau 1990; Perruchet and Pacton 2006). Essentially, opinions vary along a continuum defined by two extremes: (a) that the representations are abstract transition statistics applied implicitly with no special status for repetitions (Dienes et al. 1999); or (b) that the representations are concrete chunks or fragments applied explicitly and where repetition structure is important (Brooks and Vokey 1991; Gómez et al. 2000). This argument is also found in cross-modal transfer, where Tunney and Altmann (2001) have identified two corresponding modes of transfer: one based on sequential statistics and one based on episodic abstract analogies. In the context of probabilistic statistical learning, distinguishing between chunks and episodes is not readily possible since having some transitions more likely than others also implies repetition of small fragments. The distinction therefore rests on the application of explicit episodic memories in the perceptual judgment in the new modality vs the application of implicit more abstract representations. In our task, we attempted to reduce the likelihood of episodic memory being applied by using distractor auditory tones during the visual sequences. These made it essentially impossible for participants to use auditory mental imagery to form an explicit analogy between the auditory exposure sequence and the visual test sequences, or even explicitly recall the auditory sequence while the distractor tones were playing. In addition, when questioned in a debrief after their participation only 2 out of 36 participants (one in each group) reported any confidence in their ability to perform the visual task; the vast majority believed they were just randomly guessing, even when actually performing well above chance level. This suggests that, while explicit knowledge of the original auditory exposure sequence based on its repetition structure was likely to be present for many participants, what transferred across for use in the visual domain was primarily implicit, something also reported in other cross-modal transfer studies (Dienes and Altmann 1997). Supporting this are the results showing positive but weak correlations in both behavioural performance and neural activation, between the auditory and visual modalities. Participants who showed strong performance in the auditory modality tended on average tended to show slightly stronger performance in the visual modality as well, but it was not a strong predictor. It is therefore plausible that implicit knowledge of the structure underpinned performance in both modalities, while additional explicit knowledge was available only in the modality of initial encoding (auditory).

Intriguingly, SWS significantly enhanced performance in both tasks, in spite of only a weak relationship in performance between the tasks. If our task analysis is correct, this suggests that SWS is associated with stronger performance on both explicit and implicit components of tasks. This possibility, hinted at by our results, cannot be confirmed in our present design, but represents a potentially fruitful area of future research. It certainly raises a number of questions about the mechanism underpinning implicit memory consolidation, and whether or not the same facets of SWS are involved in consolidation of explicit and implicit memory, or if some are specialised to one type or another.

Another important way to distinguish between chunks and transition statistics is by examining the neural systems employed in the representations. In particular, Lieberman et al (Lieberman et al. 2004) have shown using an artificial grammar learning task that activation in the medial temporal lobe tends to reflect a chunking approach while activation in the striatum is associated with transition rule learning. Participants in our task were scanned with fMRI while undertaking the visual statistical learning task. Greater activation for

structured (compared to random) sequences was seen in a wide network of activation, but most strongly in the basal ganglia; especially a large striatal cluster focused on bilateral putamen but also incorporating large portions of the caudate nucleus and the globus pallidus. We did, however, also see some activation in the hippocampus which survived small-volume correction. No activation was greater anywhere in the brain for random sequences in comparison to structured sequences. These results mirror those from our unimodal auditory task (Durrant et al. 2013), as well as those from elsewhere using unimodal statistical learning (Turk-Browne et al. 2009). They suggest that abstract transition statistics are the primary mode of task completion for statistical learning, but that chunks or fragment learning does appear to play a role as well.

Significantly different patterns of activation in the 30min and 24hrs groups reveals the possible role of consolidation in cross-modal transfer. Activation in the left parahippocampus (and to a lesser extent in the right parahippocampus, though this did not survive small volume correction), specifically in the left perirhinal cortex, was stronger for structured than random sequences in the 30mins group. By contrast, activation was stronger for random than structured sequences in the 24hr group, suggesting a specific deactivation of this region after 24hrs of consolidation. An opposite pattern was seen in the left putamen, with strong activation for structured sequences occurring after 24hrs, while neither structured nor random sequences triggered activation in this region in the 30min group. This pattern is remarkably similar to that seen for the auditory test sequences in the unimodal task (Durrant et al. 2013), suggesting that it might reflect similar encoding (which should be the same for the two tasks) and similar use of the encoded information. This is also in keeping with previous studies using declarative memory tasks (Durrant and Lewis 2009; Takashima et al. 2009), which found a decrease in hippocampal activity and an increase in neocortical activity after consolidation, using a face-location association task. One important difference from our previous unimodal findings, however, is that in the cross-modal task, we see evidence of specific suppression in the MTL for random sequences in the 30min group, and for structured sequences in the 24hr group. This could be a shifted baseline reflecting non-task-specific activation in the MTL during the task (such that areas involved in task appear to be deactivated by comparison), or it could reflect inhibitory mechanisms which actively suppress particular types of sequence. It is not possible to distinguish between these alternatives in our present design.

These findings offer broad support for the standard model of consolidation (Frankland and Bontempi 2005) which proposes that the hippocampal complex plays an initial binding role connecting neocortical areas. Over time, due to the need for the hippocampus to reuse its limited storage capacity (McClelland et al. 1995), these connections are weakened and replaced by cortico-cortical connections, although the memories may not become entirely independent of the hippocampus (Nadel and Moscovitch 1997; Moscovitch and Nadel 1998). In order that external input (Robertson 2009) and internal interactions between different memory systems (Poldrack et al. 2001; Brown and Robertson 2007) should not interfere with this process, it has been proposed that it takes place during sleep (Born et al. 2006; Walker 2009). Our findings support and extend this, suggesting that this is the case not only for declarative tasks but also procedural tasks in which a transfer from the MTL to the striatum takes place over time (Reiss et al. 2005; Rieckmann et al. 2010).

In additional to examining localised activation, psychophysiological interactions were used to show differences in functional connectivity when processing structured and random sequences. Placing seeds in the left perirhinal cortex and the left putamen (the two areas shown to be sensitive to both structure and consolidation in the localisation analysis),

stronger connections were seen between the left perirhinal cortex and two areas in the anterior bilateral precuneus for structured sequences. One of these clusters also showed a functional connection with the left putamen that was related to the amount of slow wave sleep obtained. These functional connections reflect strong anatomical connections between the precuneus and both the parahippocampus and the left putamen (Zilles et al. 2003), so a clear physiological mechanism exists for this functional role. In their review and meta-analysis of the precuneus, Cavanna and Trimble (2006) suggest that it consists of two different regions which have different functional purposes. The posterior region (centred around -70mm on the anterior-posterior (y-)axis in Talairach space) is responsible for its widely-reported role in episodic memory, while the anterior region (centred around -60mm) is responsible for visuo-spatial mental imagery. Both structure-sensitive functional connections were to the latter region, suggesting that the precuneus was involved in the visuo-spatial imagery required in the task, rather than episodic memory. It has also been implicated in cross-modal transfer in a number of studies focusing mainly on visual and tactile modalities (e.g. Hadjikhani and Roland, 1998) as well as having been identified as part of a multimodal integration network (Renier et al. 2009; Sepulcre et al. 2012). Another structure also implicated in that network is the middle occipital gyrus, especially near the temporal-occipital junction (BA19) (Sepulcre et al. 2012), and we duly found stronger a functional connection between this region and the left putamen for structured than random sequences. Taken together, our functional connectivity results show clearly that structures involved in both cross-modal integration, as well as visuo-spatial imagery, are involved in cross-modal transfer in statistical learning. At least one of those connections (left putamen to anterior precuneus) may also be specifically dependent on SWS, though caution is required in interpreting this result since the average connection strength was also not significantly different between the 30min and 24hr groups. It is possible that in the immediate aftermath of learning, this connection is active while undertaking the task using visuo-spatial imagery, but not successfully tuned to performance (as the 30min group is at chance level). In the 24hr group, the connection has been modified by consolidation processes during SWS such that more SWS has strengthened the connection through reactivation (Born and Wilhelm 2012), while insufficient SWS has failed to counteract the effects of synaptic homeostasis driven by pre-task activation from the first session (Tononi and Cirelli 2014), and the connection strength is now related to subsequent performance. This intriguing hypothesis fits with our data and the iOtA theory (Lewis and Durrant 2011), but further evidence is certainly needed to confirm this.

Three important caveats in regards to our design are necessary. First is that the effects of consolidation were measured indirectly in this task, by a group comparison. This was necessary in order that the visual cross-modal transfer task remained entirely a surprise for participants (and therefore could not have an initial test on it) and ensured that they could not have attempted to modify their encoding strategy or their consolidation specifically with the task in mind. However, it does mean that comparisons are between one group of participants with 24hrs consolidation, and another with just 30mins, rather than a within-subjects comparison. This design is not uncommon in sleep research; the principal drawback is that results are likely to be conservative (i.e. a Type I error) due to the between-subjects noise. On the other hand, it can be argued that this increases the reliability of whatever effects are seen.

Second the 24hr vs 30min group design means that to some extent the effects of time and sleep are mixed together. We fully acknowledge this, but it is also worth noting that alternative designs utilising sleep deprivation or comparing day-wake to night-sleep groups would still require a group comparison, and introduce additional problems related to

circadian factors, tiredness or cognitive deficit due to sleep deprivation (if tested within 24hrs), or a weakened effect of memory due to the passage of time (if recovery nights are allowed). Given these constraints, and the need to test for an active (rather than protective) effect of sleep by using overnight polysomnography, we are confident that this 24hr design was optimal for this task. We fully acknowledge, however, that time could have played an important role in the consolidation that we witnessed, although the association with the proportion of SWS obtained suggests that time is not the only factor likely to be involved.

The second caveat regards the auditory task that preceded the visual task. In order to minimise and control task effects, we standardised the task order across participants, rather than have some participants whose auditory tasks that may have been influenced by the visual task, and some participants whose visual tasks had been influenced by the auditory task, and mixing them together in the second-level imaging analysis. However, while this ensured that the visual task remained a surprise for participants and did not influence the auditory task, the reverse is not true and it is entirely possible that performing the auditory task influenced the way the visual task was performed. Given that most participants reported having no strategy other than pure guesswork for the visual task, it seems unlikely that the preceding auditory task had a major influence on this, however it is possible that the additional exposure to 84 auditory test sequences with the same underlying transition structure could have assisted performance. Future studies could address this issue by examining cross-modal in the presence and absence of a preceding unimodal task in order to evaluate any effect that this might have. It should be emphasised, however, that both groups in our study had the same task order and design, and so the greater performance in the 24hr group, and the related imaging effects seen, cannot be due exclusively to the presence of the auditory task, or we would expect to see them in both groups. The absence of a strong correlation between the auditory and visual results similarly points to the fact that the auditory task is unlikely to be the driving force behind the visual test results.

Cross-modal transfer of statistical learning will doubtless remain an open and active topic for some time to come. The importance of statistical learning, and related mechanisms such as artificial grammar learning, is such that understanding the details of how they operate, and in particular how specific they are to the learning modality, will remain at the forefront of the science of learning and memory. In this study we have sought to introduce two additional elements to this area – sleep and consolidation – which we hope will have a bearing on the design of future empirical studies and theoretical models. We have seen a clear difference between participants who had 24hrs of consolidation rather than just 30mins. We have also seen an association of the improvement with SWS. At the neural level, we have observed an MTL-striatal trade-off remarkably similar to that seen in unimodal statistical learning, and a network of functional connectivity that involves areas of the multimodal integration network including the precuneus and the middle occipital gyrus. Taken together, these present a picture of cross-modal transfer of abstract statistical information, with both domain-specific and domain-general components.

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Tables

Table 1: *Transition Probabilities*

Prev./Next	1	2	3	4	5	6	7
1	0.0167	0.0167	0.0167	0.9000	0.0167	0.0167	0.0167
2	0.0167	0.0167	0.0167	0.0167	0.0167	0.0167	0.9000
3	0.0167	0.0167	0.0167	0.0167	0.9000	0.0167	0.0167
4	0.0167	0.0167	0.900	0.0167	0.0167	0.0167	0.0167
5	0.0167	0.0167	0.0167	0.0167	0.0167	0.9000	0.0167
6	0.0167	0.900	0.0167	0.0167	0.0167	0.0167	0.0167
7	0.9000	0.0167	0.0167	0.0167	0.0167	0.0167	0.0167

Table 2: *Behavioural Data*

Condition	Hits 30min Group	d' 30min Group	Hits 24hr Group	d' 24hr Group	*p* (**p*<0.05)
Auditory: Session 1	56.7 ± 1.33	1.008 ± 0.106	56.9 ± 1.29	0.983 ± 0.098	0.864
Auditory: Session 2	56.1 ± 1.77	0.930 ± 0.122	61.3 ± 1.33	1.394 ± 0.110	0.008*
Visual: Session 2	43.9 ± 1.10	0.119 ± 0.075	47.7 ± 1.42	0.356 ± 0.089	0.050*

Table 3: *Polysomnography Data for 24hr Group*

Parameter	Sleep Duration (mins)	Behavioural Correlation (r) (**p*<0.05)	Sleep Proportion (%)	Behavioural Correlation (r) (**p*<0.05)
N1	46.66 ± 5.53	-0.314	11.34 ± 1.45	-0.234
N2	199.65 ± 10.98	-0.274	46.92 ± 1.55	-0.328
SWS	88.79 ± 5.67	0.557*	21.74 ± 1.87	0.502*
REM	86.63 ± 9.04	-0.075	20.04 ± 1.79	-0.049

Table 4: *Main Effect of Structure - Medial Temporal Lobe and Striatum*

Anatomical Region	MNI x,y,z (mm)	# of Voxels	peak *Z*	peak *p* (unc.)
Left hippocampus	-24, -16, -17	24	4.20	< 0.0001
Left putamen	-15, 11, -2	76	5.41	< 0.0001
Right putamen	18, 8, -5	64	5.38	< 0.0001

Table 5: *Group x Structure Interaction – Whole Brain*

Anatomical Region	MNI x,y,z (mm)	# of Voxels	peak *Z*	peak *p* (unc.)
* Left parahippocampus	-18, -7, -29	10	4.08	< 0.0001
Right parahippocampus	36, -22, -26	5	3.28	< 0.0001
* Left putamen	-18, 11, 1	18	3.90	< 0.0001
Left middle temporal gyrus	-45, -43, 4	6	3.53	< 0.0001

Table 6: *PPI Analysis – Whole Brain*

Anatomical Region	MNI x,y,z (mm)	# of Voxels	peak *Z*	peak *p* (unc.)
Seed: Left parahippocampus				
Left postcentral gyrus	-57, -13, 46	34	4.09	<0.001
Right postcentral gyrus	60, -7, 40	7	3.28	<0.001
Anterior bilateral precuneus	-9, -61, 34	33	3.61	<0.001
	9, -58, 34			
Anterior bilateral precuneus	3, -43, 43	29	3.55	<0.001
	-3, -37, 42			
Seed: Left putamen				
Right middle occipital gyrus	45, -76, 10	37	3.81	<0.001
Seed: Left putamen – Correlation with SWS				
Anterior bilateral precuneus	-12, -58, 34	26	4.08	0.001

Table Captions

Table 1: Tone transition probabilities. The previous tone is given by the row number (shown) and the next tone is given by the column number (also shown). The cell indexed by these two numbers contains the conditional probability that this transition will occur given the previous tone. Each tone has one particular tone that is likely to follow it (highlighted with a darker background), but there is a small probability that one of the other six tones will follow it instead. For example, tone 3 is likely to be followed by tone 5, but it is possible for it to be followed by any of the other tones with a probability of 0.0167 each.

Table 2: Behavioural results. Scores for each condition and shown are mean number of hits ± SEM, and d' ± SEM. Significant differences between the group d' scores at the 0.05 level are indicated by an * for each condition.

Table 3: Polysomnography Results. Data are shown as mean ± SEM. EEG data from C4 referenced against the contralateral mastoid were independently scored by two experienced sleep scorers in 30s epochs according to the standardised criteria of Rechtschaffen and Kales (1968).

Table 4: Main Effect of Structure in VOIs. Data are shown for VOIs in the medial temporal lobe (bilateral hippocampus and parahippocampus) and striatum (bilateral caudate and putamen), corrected for multiple comparisons across the VOI (p_{SVC}<0.05, k=5 extent threshold).

Table 5: Group x Structure Interaction. Data are shown for the whole brain analysis (p<0.001 uncorrected, k=5 extent threshold). Clusters marked with an asterix (*) survived small-volume correction in a VOI analysis (p_{SVC}<0.05, k=5 extent threshold).

Table 6: PPI analysis. Whole brain results (p<0.001 uncorrected, k=5 extent threshold) are shown for psychophysical interactions, with seeds placed in the left parahippocampus (specifically left perirhinal cortex) and the left putamen. Correlations between functional connectivity and SWS are also shown where present.

Figure Captions

Figure 1: Experiment Design. Participants undertook an initial encoding session in which they were exposed to an auditory sequence of tones which has a particular statistical structure. After either a short (30min) or long (24hr, including sleep) delay, they were then tested on a number of short auditory tone sequences and visual sequences (circles moving across the screen), some of which shared the same statistical structure as the tone sequence and some of which were random. Brain activity was monitored during the night with polysomnography (24hr group only), and in the test session with fMRI (both groups).

Figure 2: Behavioural results (showing actual p-values to 3 d.p.). **A**: The 24hr group exhibit strong performance, while the 30min group are at chance. The difference between groups is significant (P<0.05). **B**: 24hr group performance is predicted by slow wave sleep obtained.

Figure 3: Functional imaging localisation results. **A**: Left parahippocampus (specifically left perirhinal cortex) shows decreasing involvement in processing structured sequences after 24 hours compared to 30 minutes. **B**: By contrast, left putamen shows increasing involvement. All data are shown at $p<0.05$, FWE-corrected within each VOI.

Figure 4: Functional imaging connectivity results. **A**: Functional connectivity between left perirhinal cortex and bilateral precuneus was stronger when processing structured than random sequences. **B**: Functional connectivity from left putamen to this same precuneus region was predicted by SWS obtained. All data are shown at $p<0.05$, FWE-corrected within each VOI.